HYPOXIA AS A MEDIATOR OF FOOD WEB INTERACTIONS AND ENERGY FLOW IN RESERVOIR ECOSYSTEMS

Honors Research Thesis

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INTRODUCTION

Excessive algal production (i.e., eutrophication) is a common impairment to both freshwater and coastal marine ecosystems worldwide, owing primarily to anthropogenic activities in the watershed (Breitburg et al. 2009, Rixen et al. 2010). This condition often is caused by agricultural runoff of nutrients (e.g., phosphorus, nitrogen) from the landscape in the surrounding watershed (Carpenter et al. 1998). While increased algal production can benefit ecosystems (e.g., fish production) by increasing energy availability at the base of the food web, too much algal production can harm ecosystems by enhancing microbial activity that consumes dissolved oxygen (DO), leading to hypoxic, or low-dissolved oxygen (DO < 2 mg/L), conditions (Caddy 1993, Breitburg et al. 2009).

Hypoxia generally emanates in bottom waters of an aquatic ecosystem; however, it can encompass the majority of the water column in nutrient-rich ecosystems, thus potentially affecting both pelagic (water column-oriented) and benthic (bottom-oriented) food webs (Ludsin et al. 2009, Vanderploeg et al. 2009, Zhang et al. 2009). Indeed, hypoxia can affect the distribution and movement behavior of organisms, the composition of aquatic communities, species interactions (e.g., competitive, foraging), and even energy flow through an ecosystem (e.g., Eby and Crowder 2002, Baird et al. 2004, Altieri and Witman 2006, Taylor et al. 2007, Breitburg et al. 2009).

Given that all multi-cellular organisms require oxygen to support their life functions, hypoxic areas (aka "dead zones") are considered a serious threat to the health of aquatic ecosystems. Unfortunately, the prevalence of dead zones has been increasing exponentially in coastal marine waters since the 1960s (Diaz and Rosenberg 2008) and has long plagued freshwater ecosystems, including both large lakes (Laws 1981; Ludsin et al. 2001, Hawley et al.

2006) and inland reservoirs (Coutant 1985). Further, eutrophication-driven hypoxia is expected to increase with continued climate change in freshwater and marine ecosystems alike (Ficke et al. 2007, Rabalais et al. 2010).

While all components of food webs are likely to be influenced by hypoxia (Baird et al. 1994, Wu 2002, Diaz and Rosenberg 2008), not all organisms will be affected equally, due to different levels of tolerance for low DO conditions. Major differences in tolerances of hypoxia generally exist between organisms feeding at different levels of a food web, which can alter predator-prey interactions. For example, previous investigations in the Neuse River estuary (Taylor et al. 2007), Chesapeake Bay (Ludsin et al. 2009), northern Gulf of Mexico (Zhang et al. 2009), and Lake Erie (Vanderploeg et al. 2009) reveal a greater use of hypoxic waters by small invertebrate prey species (e.g., crustacean zooplankton) than by their zooplanktivorous fish predators. This disparity in hypoxia-tolerance among organisms, in turn, holds the potential to drive seasonal variability in energy flow and production within a food web, as well as between food webs such as those found high in the water column versus those near the bottom. For instance, during normoxic (i.e., non-hypoxic) periods of the year (e.g., spring, late autumn), ample DO within the water column allows planktivorous fish and their zooplankton prey to overlap during daytime, as mobile planktivores can move throughout the water column (Ludsin et al. 2009). By contrast, when seasonal hypoxia occurs (e.g., typically during summer through early autumn), low-DO tolerant invertebrates can use hypoxic bottom waters as a refuge from visual-feeding, planktivorous fish predators that are unable to withstand hypoxia (Taylor et al. 2007, Parker-Stetter and Horne 2008, Vanderploeg et al. 2009, Zhang et al. 2009).

While no study has yet quantified the impact that this hypoxia-driven spatial disconnect between predator and prey can have on energy flow, studies have hypothesized how reduced

access to crustacean zooplankton prey (caused by formation of a hypoxic zone of refuge) can limit the production potential of zooplanktivorous fish by reducing energy intake (Ludsin et al. 2009) and energy expenditures associated with capturing sufficient prey (Taylor et al. 2007). Further, because most crustacean zooplankton prey species display diel vertical migration (DVM) behavior (i.e., predictable daily migrations from the bottom by day to the surface by night), which limits vulnerability to light-limited fish predators that depend on light to feed (Stratton and Kesler 2007, Parker-Stetter and Horne 2008, Ramcharan et al. 2001), use of a hypoxic refuge by invertebrate prey conceivably could allow these organisms to migrate between surface and bottom waters without ever being available to zooplanktivorous fish.

In such a situation, invertebrates that are tolerant of hypoxia and demonstrate DVM behavior could theoretically serve as a net energy "sink" (i.e., dead end) in the food web by moving available energy from oxygenated surface waters into hypoxic bottom waters. In turn, the energy available to planktivorous fish that can only reside above the hypoxic layer may be reduced, perhaps reducing their production potential. By contrast, without a hypoxic refuge, these same invertebrates serve as a net energy "source" in the food web. This is likely possible, owing to daily movement of invertebrates between bottom and surface waters (i.e., DVM behavior), combined with unconstrained foraging of fish.

One invertebrate that could influence aquatic food webs is *Chaoborus*, more commonly known as the phantom midge, which is prevalent in freshwater lakes and reservoirs throughout the world (e.g., He et al. 1993, Ramcharan et al. 2001, Knudsen and Larsson 2009). *Chaoborus* is an insect whose aquatic larvae 1) feed on small crustacean mesozooplankton (e.g., *Bosmina* spp., copepods, *Daphnia*) (Yan et al. 1991, He et al. 1993), 2) are tolerant of hypoxia (Stratton and Kessler 2007, Liljendahl-Nurminen et al. 2008), and 3) demonstrate strong DVM behavior

between bottom waters (by day) and surface waters (by night) (Lagergren et al. 2008, Oda and Hanazato 2008). In many natural lakes, *Chaoborus* is the dominant planktivore, even when taking into account planktivory by fish (Young and Riessen 2005).

Data from Ohio reservoirs reveal that *Chaoborus* can be high in biomass, tolerating near anoxic (DO < 0.2 mg/L) waters during the daytime, likely to escape fish predation (Devine and Vanni 2002, S. Ludsin, unpublished data); however, virtually nothing is known about the role of *Chaoborus* in reservoir food webs in Ohio, including 1) how hypoxia, mesozooplankton prey availability, and light regulate its distribution of biomass in the water column, 2) what and how much mesozooplankton prey it consumes, 3) how much it is consumed by dominant planktivorous fishes (e.g., age-0 gizzard shad *Dorosoma cepedianum*, bluegill sunfish *Lepomis macrochirus*, crappies *Pomoxis* spp.), and 4) how hypoxia can mediate its role as a sink or source of energy in the food web. These considerations are a departure from the conventional conceptualization of Ohio reservoir ecosystems (e.g., Vanni et al. 2005) for which energy flow and biomass production across the food web in these ecosystems are viewed as being regulated primarily by the gizzard shad, the dominant planktivorous fish in these ecoysystems, through a number of mechanisms, including 1) predation by young individuals on mesozooplankton that limits availability to other planktivorous fishes and 2) excretion of nutrients into the water column by adults following foraging on bottom sediments (Stein et al. 1995, Vanni et al. 2005).

While this current conceptual model of Ohio reservoirs seems intuitive during non-hypoxic periods, its applicability is questionable when hypoxia occurs, which in Ohio reservoirs, means the large majority of the growing season (i.e., late spring through early summer; S. Ludsin and Ohio Division of Wildlife, unpublished data). Given that fish do not appear capable of using

the hypoxic zone, whereas *Chaoborus* use it for refuge during the day, the role of *Chaoborus* in Ohio reservoir food webs is likely being underplayed.

I expect that *Chaoborus'* higher tolerance of low DO, combined with its tactile (versus visual) feeding strategy (Swift and Fedorenko 1975), would allow it to use the hypoxic hypolimnion as a refuge from visual predators (i.e., planktivorous fish) during the day and forage on mesozooplankton in the epilimnion at night when predation risk is low (due to low ambient light). If true, *Chaoborus* would serve as a net energy sink during hypoxic periods through its transfer of energy from the epilimnion into the hypolimnion during the day, where it is invulnerable to predators. Further, the loss of mesozooplankton energy available to other planktivores in the epilimnion (e.g., larval and young juvenile fish such as gizzard shad, white and black crappie, and bluegill) might have a negative effect on their ability to forage and grow.

My primary goal is to determine how hypoxia and *Chaoborus* interact to drive pelagic food web interactions, energy flow, and habitat quality for planktivorous fishes. Toward this end, I sampled an Ohio reservoir before, during, and after peak hypoxia in 2011, focusing on spatial overlap and trophic interactions between *Chaoborus*, their mesozooplankton prey, and planktivorous fish predators. Herein, I only report findings on the spatial distribution of these organisms in relation to hypoxia and light, as well as on the potential for *Chaoborus* to regulate mesozooplankton availability through predation.

METHODS

Study system

Field collections were made during 2011 in Hoover Reservoir (Delaware and Franklin counties, OH). Hoover Reservoir is a eutrophic impoundment of Upper Big Walnut Creek that

supplies drinking water to Franklin County area. This reservoir has a surface area of 1,140 ha, a mean depth of ~5.7 m (maximum = 20.9 m), and a 495-km^2 watershed that is predominantly agricultural (72%), with some forest (24%). As with most other tributary reservoirs in Ohio, Hoover is dominated by gizzard shad, an omnivorous fish positioned in the middle of the food web (Stein et al. 1995, Bremigan and Stein 2001). In addition to acting as a consumer of mesozooplankton, age-0 gizzard shad serve as the primary prey for top predators in Ohio reservoirs such as Hoover, including a variety of economically important sportfish (e.g., saugeye *Sander canadensis* x *S. vitreus*; Storck 1986, DiCenzo et al. 1996, Michaletz 1997, Michaletz 1997). Other species in Hoover Reservoir (and other Ohio tributaries) include bluegill sunfish, white and black crappie (*Pomoxis annularis* and *P. nigromaculatus*), and white bass (*Morone chrysops*).

Field Sampling

General field design. As with other moderately deep north-temperate reservoirs and natural lakes (e.g., Winner et al. 1962), Hoover Reservoir becomes thermal stratified during late spring through early fall, with the hypolimnion generally becoming hypoxic during this time (Ohio Department of Natural Resources, Division of Wildlife, unpublished data). Because hypoxia influences movement, spatial overlap, and predator-prey interactions of zooplanktivorous fishes and their prey in other freshwater and marine ecosystems (e.g., Taylor et al. 2007, Roberts et al. 2009, Ludsin et al. 2009, Zhang et al. 2009), I sampled three dates during 2011 to represent pre-, peak-, and post-hypoxia. I sampled on 10 May 2011, when the water column was thermally stratified but bottom waters had not yet become hypoxic (Figure 1a; Table 1). I sampled again on 1 August 2011 during peak thermal stratification and hypolimnetic hypoxia (Figure 1b; Table 2). Finally, I sampled on 3 November 2011, after the hypoxic bottom

layer had disappeared and temperature had become uniform throughout the water column (Figure 1c; Table 3).

Sampling occurred at two replicate stations in Hoover, site A (40 07.4436 N, 82 52.7441 W) and B (40 07.1677 N, 82 52.797 W), both located in the middle portion of the reservoir in ~10 m of water. Sampling on all dates began during early afternoon (~12:00) and continued through dusk into the middle of the night (~23:30). As described below, I collected information on water quality, zooplankton (mesozooplankton and their primary invertebrate predator, *Chaoborus*), and planktivorous fish, using identical methods on each date.

Water quality. To quantify the physical and chemical environment, vertical profiles of the water column (from the surface to ~ 1 m from the bottom) were conducted at 1-m increments during daylight hours. Measurements of temperature (nearest 0.1^0C), DO (nearest 0.1 mg/L), and light (ambient photosynthetically active radiation, PAR; in µmol photons/m^2/s) were collected at both sites using a YSI (Yellow Springs Instruments) sonde and LICOR sensor.

Zooplankton. Discrete-depth pump sampling (Pangle et al. 2007, Vanderploeg et al. 2009) was used to collect *Chaoborus* and smaller crustacean (i.e *Bosmina* spp., calanoid and cyclopoid copepods, *Daphnia* spp.) and rotifer mesozooplankton at both stationary locations. I sampled 1 m^3 of water within 2 or 3 discrete layers of the water column, depending on the sampling date. The thickness of each layer was determined from the YSI sonde profiles, which were taken just before zooplankton pump sampling began. During May and November, when no hypoxia occurred, water was pumped from both the epilimnion (top 5 m of the water column) and the hypolimnion (bottom 5 m of the water column). During August, when hypoxia was present, water was pumped from three discrete layers, the epilimnion (top 4 m of the water column), the metalimnion (thermocline region; middle 5-6 m depth), and the hypolimnion

(bottom 4 m), (Figure 1b). I sampled the thermocline region during August because both planktivorous fish and zooplankton can aggregate there during the day when their normal bottom refuge becomes hypoxic (Vanderploeg et al. 2009; S. Ludsin, unpublished data). During all three sampling events, each layer of the water column, at both sites, was sampled during the day (> 1 h before twilight) and during the night (> 1 h after twilight). In most instances, two replicate sets of pump samples were collected at each site, unless restricted by time or adverse weather conditions, in which case only one replicate was collected per site (May night samples, August day and night samples).

Pump sampling was supplemented with vertical net tows conducted at night, using a metered 0.5-m diameter zooplankton net (500-µm mesh). I towed nets to collect *Chaoborus* for density and biomass estimation and diet analysis, as *Chaoborus* can burrow in the sediments during the day (Haney et al. 1990). Duplicate net tows were conducted during May and August at each site, with three replicates being conducted at each site in November, owing to conspicuously low *Chaoborus* numbers.

All invertebrate samples were preserved in 10% sugar formalin with the addition of Lugol's solution to prevent *Chaoborus* regurgitation (Moore et al. 1994), with the exception of May samples, during which time Lugol's solution was not used. Samples were stored until processing in the laboratory.

Planktivorous fish. Fish were collected on all three dates at each site in accordance with the Institutional Animal Care and Use Committee IACUC protocol #2009A0089. Similar to zooplankton pump collections, I sought to collect planktivorous fishes from above and below the thermocline during the daytime (> 1 h before twilight) and nighttime (> 1 h after twilight), using YSI profiles as a guide. Midwater trawling (n = 2-3 replicate tows per layer per time period) was

conducted using the RV *Echo*. During each tow, two 1-m x 1-m, metered frame trawls (6.4-mm mesh) were deployed, providing duplicate collections. Each tow lasted 6-10 min with each net straining between 480 and 1560 m^3 of water (tow speed = 1.5-2.0 m/s). Oblique tows were conducted within each layer of the water column such that the trawls were stepped up at 1-m intervals from the deepest depth in each layer to the uppermost bin (with equal time spent at each 1-m interval within a layer). Owing to the need for the trawls to pass through the uppermost portion of the water column, the possibility exists that some fish residing in surface waters (epilimnion) were collected in tows associated with the bottom layer (hypolimnion). Any captured larval fish were preserved in 95% ethanol for laboratory identification (following the methods of Auer 1982), whereas age-0 juveniles were identified and counted in the field and preserved on ice until stored in a -10^0 C freezer for laboratory analysis.

Laboratory methods

Zooplankton enumeration. To determine invertebrate species composition, zooplankton pump samples were counted and individuals were identified at the species level, or genus level for *Daphnia*. Measures of individual length, egg number, and total species or genus abundance were recorded. Total species or genus biomass, density, and productivity were then calculated (Culver 1985, Kane 2004). In general, I counted a minimum of 100 individuals per taxon in at least 9 ml of the sample to estimate density and measured the total length (TL) of up to 20 individuals per taxon per sample. Total lengths were converted to dry mass (Culver 1985) and productivity was estimated using information on species-specific egg counts, sex ratios, and temperature (Frost 1997).

In addition to counting and measuring head length and TL (nearest 0.1 mm) of all *Chaoborus* in pump samples, I counted all *Chaoborus* in net tows and measured a random

subsample of 50 random individuals. Individuals were categorized into four development stages, based on size. Because water-column sampling during the day may underestimate *Chaoborus* density, owing to burrowing in the sediments during the day, I used my nighttime vertical net tows to estimate *Chaoborus* density in each depth layer at each site on each date. To do so, I multiplied my mean *Chaoborus* density from my replicate nighttime tows from each site by the proportional abundance of *Chaoborus* in the discrete-depth pump samples (whether collected during the day or night).

Chaoborus consumption. Diet analyses on *Chaoborus* were conducted to estimate their consumption of different zooplankton prey (and hence, energy intake). *Chaoborus* diet analyses were conducted using a compound microscope with 50x magnification, guided by the methods of Swift and Fedorenko (1973). Individual *Chaoborus* lengths were multiplied by a factor of 1.08 to correct for formalin shrinkage (Lazenby et al. 1994) and then converted to dry mass (nearest 0.001 mg), (Chimney et al. 2007). For pump samples, a random sample of *Chaoborus* diets was analyzed until 10 non-empty diets were attained or until 20 individuals were analyzed (if the minimum of 10 non-empty diets was not achieved). For vertical net tow samples, a subsample of 30 *Chaoborus* diets was analyzed. Prey consumed were identified to the genus level and prey TL was recorded when an accurate measure was possible.

Statistical Analysis

To quantify differences in zooplankton biomass, two-way analysis of variance (ANOVA) was used. Because unequal numbers of layers existed between sampling dates (i.e., May and November had two depth layers, whereas August had three depth layers), sampling dates were analyzed separately. These two-way ANOVAs were used to quantify differences between day and night, between layers of the water column, and whether their interaction was significant.

Any significant trends were further analyzed with a Tukey's honestly significant difference post-hoc test.

To quantify differences in *Chaoborus*, multiple approaches were used. First, I used one-way ANOVA to test for biomass differences among sampling dates, followed by Tukey's hsd comparisons. To quantify proportional differences in *Chaoborus* in the epilimnion (and concomitantly the hypolimnion) between day and night in May and November, I used a two-sample t-test. For August, I used a two-way ANOVA to contrast proportional differences among depth layers (epilimnion, metalimnion, hypolimnion) between day and night. Significant effects were further analyzed using Tukey's hsd comparisons. Two-way ANOVAs were used to determine differences in *Chaoborus* TL and dry mass between day and night and between layers of the water column, accounting as well for any interaction between the two variables. Any significant differences were analyzed using Tukey's hsd comparisons. In November, no *Chaoborus* were caught in the epilimnion, thus a two-sample t-test was used to analyze TL and wet mass differences between night and day.

Similar methods were used for analyzing fish data. Two-way ANOVAs were performed for each month to determine differences between sites (A, B), layers of the water column (epilimnion, metaliminion, hypolimnion), and time of day (day, night), along with determining any second-order interactions between time of day, site, and layer. Significant results were then analyzed using Tukey's hsd comparisons.

All data were tested for normality (Kolmogorov-Smirnov normality tests), with some attributes being transformed prior to analysis (i.e.., proportional depth data and *Chaoborus* diet biomass data were arcsin-square root transformed; fish density data were $\log_{10}$ transformed) to achieve normality (all data were normal with all $p > 0.1$). Cochran's C and Levene's Test were

used to assess homogeneity of variances. For all analyses, p-values less than 0.05 were considered significant.

RESULTS

Physical Conditions

Temperature, DO, and light level varied among months (Table 1). Temperature data during May, averaged between sites A and B, reveal slight stratification of the water column, with a mean temperature difference of 2.3°C between warmer, epilimnetic waters and cooler, hypolimnetic waters (Table 1, Figure 1). Although DO was higher in the epilimnion than in the hypolimnion, no hypoxia (DO < 2 mg/L) occurred within the water column at any depth (Table 1, Figure 1a). As expected in a turbid, eutrophic reservoir such as Hoover, light availability (as measured by photosynthetically active radiation, PAR) decreased exponentially with depth, with light levels suitable for fish planktivory (PAR < 0.2 μmol photons/m^2/s; Vanderploeg et al. 2009) only occurring at < 4 m depth (Table 1; Figure 1a).

August profiles demonstrate clear temperature and DO stratification within the water column, as well as variable light conditions from surface to bottom (Figure 1). Water temperature was highest in the epilimnion, intermediate in the metalimnion, and lowest in the hypolimnion (Table 1; Figure 1b). Hypoxia occurred during August, but only in the hypolimnion, with epilimnetic DO being uniformly high and metalimnetic DO ranging from 4.8 mg/L at 4 m depth to 1.7 mg/L at 6 m depth (Table 1, Figure 1b). Light demonstrated a similar pattern as in May, only reaching levels below which planktivores likely can feed at 5 m depth (Figure 1b).

Physical and chemical conditions differed in November relative to previous months (Table 1; Figure 1c). During November, the water column was isothermal, varying by < 0.2°C from surface to bottom. Additionally, DO was relatively constant and well-oxygenated throughout the entire water column (varying from 6.1 to 5.7 mg/L from surface to bottom). While light demonstrated an exponential decline from surface to bottom, levels < 0.2 μmol photons/m^2/s, which can reduce the ability of planktivorous fish to feed (Vanderploeg et al. 2009), were not documented at any depth in the water column.

Mesozooplankton & Chaoborus *Biomass Distribution*

Mesozooplankton prey. The mesozooplankton community, which I defined as crustacean zooplankton and rotifer species in *Chaoborus* diets (see below), did not vary considerably through time (one-way ANOVA: $F_{2,5} = 7.9.$; $p = 0.64$), despite an apparent increasing trend through time in mean (± 1 standard deviation, SD) total biomass during May (10.5 ± 4.7 mg/L), August (21.1 ± 1.0 mg/L), and November (51.8 ± 25.6 mg/L). Species composition, however, did vary through time (Table 2). During May, the zooplankton community was dominated primarily by cyclopoids (39% by dry biomass), calanoids (35%), and *Daphnia* spp. (21%), with other cladocerans and rotifers being less abundant (Table 2). The taxonomic composition varied only slightly during May through August; calanoids and cyclopoids still dominated biomass (82% of the community by dry biomass), with *Daphnia* spp., other cladocerans and rotifers being less available (Table 2). November showed more variation, as calanoids and *Daphnia* dominated (75% of dry biomass) with smaller biomasses of cycloids and rotifers.

The vertical distribution of mesozooplankton taxa important to *Chaoborus* also varied through time, as well as between layers within months. In May, zooplankton biomass did not differ between day and night ($F_{1,7} = 0.50$, $p = 0.52$) or between the upper and lower layers of the

water column ($F_{1,7} = 4.89$, $p = 0.09$) (Figure 2a). In addition, no interaction between time of day (day versus night) and water-column layer (epilimnion versus hypolimnion) occurred ($F_{1,7} = 0.42$, $p = 0.55$). Similarly, in November, zooplankton biomass numbers did not differ between day and night ($F_{1,7} = 2.88$, $p = 0.16$) or between layers of the water column ($F_{1,7} = 1.28$, $p = 0.32$), nor was there an interaction between the these factors ($F_{1,7} = 0.57$, $p = 0.49$) (Figure 2b). By contrast, some differences were found during August (Figure 2c). While zooplankton biomass did not differ between day and night ($F_{1,7} = 0.30$, $p = 0.60$) and an interaction between time of day and water-column layer was not detected ($F_{1,7} = 1.27$, $p = 0.35$), the distribution of biomass varied among the three water-column layers ($F_{1,7} = 45.56$, $p = 0.0002$). Tukey's post-hoc comparisons revealed that zooplankton biomass declined from the epilimnion to the metalimnion to the hypolimnion (Figure 2a), revealing that mesozooplankton were less abundant in the hypoxic layer of the water column.

Chaoborus. Only *Chaoborus punctipennis*, a species common to lake and reservoir ecosystems throughout North America (Bass and Sweet 1984, Moore 1988), was sampled. Similar to mesozooplankton biomass density, *Chaoborus* density (and biomass density; K. Lang, unpublished data)—based on nighttime vertical tows—varied across months (one-way ANOVA: $F_{1,5} = 15.79$, $p = 0.026$). Mean density in August (227 ± 38 individuals/m^3) and November (29 ± 17 individuals/m^3) differed, with density in May being intermediate but not statistically different from either other month (Tukey's hsd comparisons). The vertical distribution of *Chaoborus* in the water column varied both across months and within months (Figure 3). During May (t-test: $t = 2.16$, $p = 0.16$) and November (t-test: $t = 2.10$, $p = 0.17$), proportional distribution of *Chaoborus* density (or biomass density) did not differ in the water column (epilimnion versus hypolimnion) or between day and night (Figure 3a,b). During August, however, when severe

hypoxia occurred, the vertical distribution of *Chaoborus* differed among water-column layers (one-way ANOVA: $F_{1,11} = 8.74$, $p = 0.02$), with higher density in the epilimnion (on average) than in the hypolimnion (Figure 3d). The magnitude of this difference among layers, however, varied between day and night (layer x time interaction; $F_{1,11} = 5.49$, $p = 0.04$). Tukey's pairwise comparisons revealed that *Chaoborus* density was greater in the epilimnion during night than the metalimnion or hypolimnion during the night, with proportional densities not differing elsewhere (Figure 3c).

Based on individuals collected in nighttime vertical tows, *Chaoborus* mean TL ($F_{1,5} = 11.71$, $p = 0.04$) and dry mass ($F_{1,5} = 18.49$, $p = 0.02$) varied among months. Mean TL and dry mass were greater during May (TL± SD = 9.1 ± 0.2 mm; dry mass = 0.29± 0.02 mg), as compared to August (TL = 7.8 ± 0.4 mm; dry mass = 0.20± 0.02 mg), with November TL and mass (TL = 8.7 ± 0.1 mm; dry mass = 0.25± 0.00 mg) falling intermediate and did not differ from May or August based on Tukey's post-hoc comparisons.

During May, the *Chaoborus* population consisted almost entirely of 4th instar individuals (0.7% 3rd instar), with mean TL not differing between collections made between the epilimnion and hypolimnion ($F_{1,6} = 2.53$, $p = 0.22$) or between day and night ($F_{1,6} = 0.0078$, $p = 0.94$). Further, no layer x time interaction occurred ($F_{1,6} = 0.13$, $p = 0.74$). Dry mass (0.29 ± 0.02 mg), did not differ with layer ($F_{1,6} = 3.35$, $p = 0.16$), or time of day ($F_{1,6} = 0.022$, $p = 0.89$); no interaction between them occurred ($F_{1,6} = 0.10$, $p = 0.77$). Similar results were observed during November, with mean TL and mean dry mass not differing between day and night (t-test: both $t \leq 0.10$, both $p \geq 0.93$). During this time, most of *Chaoborus* were 4th instars (99% of individuals), with the rest being 3rd instars. A comparison by depth was not possible in November, as no *Chaoborus* were captured in the epilimnion. During August, no differences in

Chaoborus TL or dry mass was observed between day and night ($F_{1,9} \leq 2.79$, both $p \geq 0.17$), nor was a layer x time interaction detected ($F_{1,9} \leq 0.65$, both $p \geq 0.57$). However, differences in mean TL and dry mass among layers existed ($F_{1,9} \geq 8.68$, both $p \leq 0.04$) such that longer (and heavier) *Chaoborus* were found in the hypolimnion (TL = 7.8 ± 0.1 mm; dry mass = 0.20± 0.06 mg) relative to the epilimnion (TL = 3.8 ± 1.5 mm; dry mass = 0.03± 0.03 mg). During this time, most of the sampled *Chaoborus* population consisted of 4th instars (42.8% of individuals), but 1st (9.5 % of individuals), 2nd (21.5 % of individuals), and 3rd (25.5% of individuals) instars also were detected.

Chaoborus *Consumption*

Empty crops. *Chaoborus* foraging varied among months and between daytime versus nighttime (Figure 4). Overall, the mean (± 1 SD) proportion of individuals with empty stomachs did not differ among May (0.59 ± 0.17), August (0.43 ± 0.10), and November (0.59 ± 0.05 (one-way ANOVA: $F_{2,5} = 1.21$, $p = 0.41$). Likewise, no differences in this attribute occurred between day and night for any month (two-sample t-tests; all $t \leq 2.99$, all $p \geq 0.10$; Figure 4). Despite statistical non-significance, during May, *Chaoborus* fed primarily at night; > 93% of the individuals had an empty crop during the day, whereas > 52% had prey in their crop during the night (Figure 4a). Similar results were observed for November, with > 87% of individuals having an empty crop during the day and > 47% of individuals had prey in their crop during night (Figure 4c). During August, diel differences in foraging were less obvious with 44% and 65% of the individuals collected during the day and night, having food in their crop (Figure 4b). Those individuals feeding during the day in August were found primarily above the hypoxic hypolimnion (K. Lang, unpublished data).

Crop biomass. For individuals that consumed zooplankton, I estimated mean (± 1 SD) mass-specific consumption (mg stomach dry mass / mg *Chaoborus* dry mass), finding it to be higher during August (1.57 ± 0.05 mg/mg) than during either May (0.50 ± 0.18 mg/mg) or November (0.59 ± 0.06 mg/mg), with these latter two months not differing (one-way ANOVA with Tukey's hsd comparisons: $F_{2,5} = 28.3$, $p = 0.01$). Mass-specific consumption, however, did not differ between day and night ($0.14 \leq p \leq 0.71$) or between water-column layers for any of the months when analyzed individually (both $p \geq 0.67$; *Chaoborus* occurred only in the epilimnion during November, preventing a comparison). No layer x time interactions was evident either during May or August (both $p \geq 0.51$).

Diet diversity. *Chaoborus* consumed a diversity of mesozooplankton taxa (Figure 5). The proportional biomass of each taxon (based on dry mass) varied little among months, with calanoids, cyclopoids, and *Daphnia* dominating diets. In May and August, calanoids comprised the largest fraction of my *Chaoborus* diets (71% and 49%, respectively), followed by cyclopoids (15% and 34%, respectively). November, however, revealed a different pattern; *Daphnia* contributed 58% of the diet, followed by cyclopoids (36%) and calanoids (4%). The decrease in calanoid consumption does not correlate with a decrease in calanoid presence in the water column, as biomass remained high (Figure 5).

Taxon selectivity. Selectivity by *Chaoborus* larvae may differ among months. In May, calanoids appear to be consumed in greater proportion than expected based on their ambient biomass, whereas cyclopoids represent a much smaller portion of *Chaoborus* diet than might be expected given their high biomass in the water column (Figure 5). By contrast, during August, the biomass consumed for each taxon appeared to correlate well with the biomass present in the water column for these taxa, suggesting little selectivity. In November, *Chaoborus* appear to

select for *Daphnia*, as the proportion consumed was greater than the proportion present in the water column. By contrast, calanoids represent only a small fraction of diet, despite ambient biomass being high during this month (Figure 5).

Daily consumption estimation. Combining *Chaoborus* diets (e.g., diel feeding behavior, proportion of empty stomachs, average stomach biomass) and density with evacuation rates of zooplankton in *Chaoborus* crops (Moore 1988), I estimated total daily consumption of zooplankton ($mg/m^3/d$) during each month for the sampled *Chaoborus* population. During May, zooplankton consumption (averaged across sites) was 1.43 and 2.75 $mg/m^3/d$ when accounting for or not accounting for empty crops, respectively. These consumption estimates represented 77% and 148% of the total available zooplankton production in May when empty *Chaoborus* stomachs were factored or not factored into the analysis, respectively (Figure 6). During August, total consumption of zooplankton (averaged across sites) was 5.63 and 10.63 $mg/m^3/d$ when accounting for or not accounting for empty stomachs, respectively. These consumption estimates represented 53% and 100% of the total available zooplankton production in August when empty *Chaoborus* stomachs were factored or not factored into the analysis, respectively (Figure 6). The estimated impact of *Chaoborus* consumption on zooplankton production was much lower during November. Total consumption of zooplankton (averaged across sites) was 0.32 and 0.68 $mg/m^3/d$ when accounting for or not accounting for empty stomachs, respectively. These consumption estimates respectively represented only 4% and 10% of the total available zooplankton production in November when empty *Chaoborus* stomachs were factored or not factored into the analysis (Figure 6).

Fish Composition and Distribution

Fish collected in the midwater trawls consisted primarily (87-99% of catches) of gizzard shad, white and black crappies, bluegill sunfish, and white bass (Figure 7). During May, the largest proportion of the catch was comprised of age 1+ black and white crappies, followed by age 1+ gizzard shad, whereas during August, the fish catch consisted of a combination of species, including bluegill, crappie, gizzard shad, and white bass. All of the fish collected during August were young-of-year (age-0). Only in November did I find midwater trawls dominated by age-0 gizzard shad, with age-0 crappies comprising nearly all of the remainder of the catch (Figure 7).

Similar to the lower food web, the total catch of fish varied within and among months. During May, fish density did not differ between sampling sites ($F_{1,19} = 0.89$, $p = 0.36$) or between water-column layers ($F_{1,19} = 4.37$, $p = 0.06$). However, mean fish density was significantly higher during the nighttime than daytime ($F_{1,19} = 5.18$, $p = 0.04$), although the magnitude of this difference varied with water-column layer (layer x time interaction; $F_{1,19} = 24.31$, $p < 0.0003$). Specifically, I found that fish density was lower in the epilimnion during the day, as compared to the epilimnion during the night or the hypolimnion during both day and night (Figure 8).

During August, fish density did not differ between sampling sites ($F_{1,16} = 1.35$, $p = 0.27$), nor was an interaction between time of day and layer of the water column evident ($F_{1,16} = 2.33$, $p = 0.16$). However, differences in catches between day and night ($F_{1,16} = 5.99$, $p = 0.04$) and between water-column layers ($F_{1,16} = 30.61$, $p = 0.0003$) were detected. Similar to May, fish density was greater at night than during the day during August ($F_{1,16} = 5.99$, $p=0.036$). Unlike

May, however, fish density was greater in the epilimnion than in the hypolimnion during August, when hypolimnetic hypoxia existed (Figure 8).

In November, fish densities did not differ between sampling sites ($F_{1,15} = 0.12$, $p = 0.73$), again confirming that these sites served as good replicates across all months. Fish density did differ, however, between day and night ($F_{1,15} = 206.86$, $p < 0.0001$), between layers of the water column ($F_{1,15} = 33.62$, $p < 0.0003$), and a significant interaction between time of day and water-column layer existed ($F_{1,15} = 33.62$, $p < 0.0003$). Day and night catches differed because no fish were caught during the day. Further, Tukey's post-hoc comparisons revealed that more fish were caught in the hypolimnion than in the epilimnion during night, which underlies the significant interaction term (Figure 8).

Spatial Overlap of the Food Web

Daytime distributions. When mesozooplankton biomass, *Chaoborus* density, and fish density were combined by month, clear patterns in habitat use and spatial overlap became evident (Figure 9). During the daytime in normoxic May (Table 1), mesozooplankton biomass was greater in the epilimnion than the hypolimnion, although the difference was not statistically significant (see above), and fish and *Chaoborus* had similar distributions between layers (Figure 9a). During the day in August, when hypoxia was at its maximum (see Table 1), biomass was significantly higher in the epilimnion as compared to the hypolimnion for fish, *Chaoborus*, and zooplankton (Figure 9c). During normoxic November during the day, mesozooplankton were more associated with the epilimnion than the hypolimnion (although not statistically significant), whereas *Chaoborus* and fish occurred only in the hypolimnion (Figure 9e).

Nighttime distributions. Comparisons of species distributions between day (Figure 9a,c,e) and night (Figure 9b,d,f) for each month demonstrate the impact of hypoxia on diel

movement patterns. During May, clear DVM behavior from the hypolimnion to the epilimnion was evident for both fish and *Chaoborus* from day (Figure 9a) into night (Figure 9b), whereas mesozooplankton continued to remain epilimnion (Figure 9a,b). During hypoxic August, fish and zooplankton distributions remain fairly constant between day and night, with both remaining primarily in the oxygenated epilimnion (Figure 9c,d). *Chaoborus*, however, showed some degree of DVM behavior, occupying all layers of the water column during the day, but then migrating primarily into the epilimnion at night (Figure 9c,d). During November, when the entire water column was normoxic and light (PAR) also penetrated to the lake bottom (see Figure 1c), all organisms tended to use the hypolimnion at night (Figure 9f) more than in May (Figure 9b) or August (Figure 9d) with the degree of DVM behavior being lower than in May (Figure 9a,b) for all *Chaoborus*.

DISCUSSION

Herein, I sought to determine how hypoxia affects reservoir food webs through changes in interspecific interactions, as hypoxic conditions have been shown to affect fish and invertebrate vertical and horizontal distributions in other ecosystems (Haney et al. 1990, Horpilla et al. 2000, Marcus 2001, Eby and Crowder 2002, Stratton and Kessler 2007, Kimmel et al. 2009, Ludsin et al. 2009, Zhang et al. 2009). I was particularly interested in learning how hypoxia might mediate energy flow through the food web by altering predator-prey interactions involving *Chaoborus*, a species that is more tolerant of hypoxia than its mesozooplankton prey or fish predators (Horpilla et al. 2000, Stratton and Kessler 2007).

To explore the effect of hypoxia energy flow through the pelagic food web, I contrasted the vertical distribution of *Chaoborus*, their mesozooplankton prey, and planktivorous fish

before, during, and after hypoxia. I also quantified consumption of zooplankton by *Chaoborus* among these same periods and compared it to zooplankton production.

Overall, my results partially support my hypotheses in that I found 1) changes in species distributions in response to hypoxia, 2) higher *Chaoborus* crop biomass estimates during peak hypoxia than during normoxic months, and 3) high levels of estimated zooplankton consumption by *Chaoborus*, thus likely reducing food availability to other planktivores. Below, I discuss these findings more fully.

Mesozooplankton. Crustacean mesozooplankton, which dominated the diets of *Chaoborus* (and age-0 gizzard shad; K. Lang, unpublished data) display DVM behavior in the presence of predation risk, wherein they generally take refuge from visual predators in bottom waters during the day, only moving to the surface at night to feed or access warmer temperatures (Vanderploeg 2009). However, pump sampling at discrete layers of the water column demonstrated that mesozooplankton did not display normal DVM behavior, as its biomass was generally dispersed throughout the entire water column during both normoxic May and November. Further, during hypoxic August, I found significantly greater mesozooplankton biomass in the epilimnion than in either the metalimnion or hypolimnion, despite light levels in hypolimnion (PAR = 0.04 μmol photons/m^2/s) being lower than in the epilimnion (PAR >28 μmol photons/m^2/s).

Both hypoxia and *Chaoborus* distributions likely drive this behavior during August. Perhaps mesozooplankton in Ohio reservoirs are intolerant of the hypoxia, forcing mesozooplankton to aggregate in the oxygenated metalimnetic and epilimnetic waters during August. Such behavior has been documented in other systems, both freshwater (Vanderploeg et al. 2009) and marine (Marcus 2001, Kimmel et al. 2009). If so, this would suggest that the net

costs associated with living in the hypoxic hypolimmion must outweigh net costs associated with living in the epilimnion.

While the true net costs associated with living in the hypolimnion versus epiliminion during August in Hoover are unknown, prolonged exposure to hypoxia can lead to reduced fitness through reduced fecundity, as well as increased mortality (Stalder and Marcus 2009). Further, while light levels were lower in the hypolimnion (< 0.04 μmol photons/m^2/s) than in the epilimnion (< 28 μmol photons/m^2/s) during August, which suggests that the risk of predation would be lower in the hypolimnion than epilimnion (Vanderploeg et al. 2009), this might not necessarily be true. Admittedly, the density of planktivorous fish was higher in the epilimnion than the hypolimnion in August; however, this risk might be offset by the fact that large *Chaoborus* were in higher abundance in the hypolimnion than epiliminion during August. Because *Chaoborus* are tactile feeders, and thus rely on sensory cues other than vision to forage, the hypoxic refuge may not be a refuge at all for mesozooplankton. In turn, with predation risk potentially being equal above (due to planktivorous fish and small *Chaoborus*) and below (due to large *Chaoborus*) the oxycline, I suggest that fitness costs associated with hypoxia exposure underlies the higher use of epilimnetic waters during the day in August.

The lack of a conspicuous DVM during May and November can be explained more simply. During these normoxic months, both *Chaoborus* and planktivorous fish (May) or just *Chaoborus* (November) were residing in the lower half of the water column, likely using the low light conditions as a refuge from their own predators. Thus, the safest place for mesozooplankton to reside is seemingly the epilimnion. Indeed such "reverse" DVM behavior has been observed in other ecosystem with tactile predators such as *Chaoborus* (Frost and Bollens 1992).

Chaoborus. *Chaoborus* larvae display DVM, seeking refuge from visual fish predators during the day in the hypolimnion, where light levels are too low for fish to forage, and then coming to the surface at night to feed (Stratton and Kessler 2007). This behavioral pattern, however, takes on another element during times of hypoxia. *Chaoborus* are more tolerant of hypoxic conditions than fish (Horpilla et al. 2000, Stratton and Kessler 2007). In turn, during hypoxia, the hypolimnion becomes an even more secure refuge from predation. Despite *Chaoborus* tolerance of hypoxic conditions, some have suggested that it may in fact be more energetically efficient to remain in the epilimnion during times of hypoxia (Swift 1976). Thus, two distinct possibilities arise when considering hypoxia-induced behavioral effects on *Chaoborus*.

In Hoover Reservoir, *Chaoborus* used all layers of the water column, with fairly equal distributions between the upper and lower layers during May and statistically non-significant higher biomass in the hypolimnion as compared to the epilimnion during November. During hypoxic August, *Chaoborus* biomass was higher in the epilimnion and use of the hypolimnion decreased, as it did for zooplankton and fish. This trend of high *Chaoborus* densities in the epilimnion was explained partially by vertical migration inoto the epilimnion at night. Observed *Choaoborus* presence in the epilimnion during the day was unexpected, yet may be explained by several factors. First, it may be energetically more efficient and beneficial to remain in the epilimnion during the day where prey is abundant and DO conditions are less demanding than to migrate between water-column layers (Swift 1976). Second, *Chaoborus* sampled from the epilimnion were significantly smaller than those from the hypolimnion, which is consistent with Stratton and Kessler's (2007) suggestion that smaller *Chaoborus* may be less vulnerable to predation in the epilimnion than larger individuals. Finally, sampling bias may play a role.

Although greater numbers of *Chaoborus* were observed in the epilimnion as compared to the hypolimnion, hypolimnetic abundance may be underestimated as *Chaoborus* are known to burrow in sediment (Haney et al. 1990).

These observations have major implications regarding *Chaoborus'* potential impact on Hoover's pelagic food web. First, during hypoxic August, *Chaoborus* remained in high numbers at the epilimnion during the day where potential planktivorous fish predators also were in high abundance and light was sufficient (PAR >0.02 μmol photons/m^2/s) to promote fish planktivory (Vanderploeg et al. 2009). In this way, hypoxia may promote fish growth via increased access to *Chaoborus* as prey. This enhancement of prey to fish consumers in Hoover Reservoir is analogous to hypotheses generated in Lake Erie (Brandt et al. 2009) and Chesapeake Bay (Costantini et al. 2008) that have argued that hypoxia can benefit higher consumers (i.e., piscivorous fish) by removing the bottom as a refuge for their planktivore prey (a phenomenon that I also observed during August). I am currently testing this hypothesis by exploring the diets of planktivores (e.g., gizzard shad, crappies, bluegill, and white bass) that were collected during my midwater trawl surveys (K. Lang, unpublished data).

This enhanced overlap between *Chaoborus* and planktivorous fish during the day in August also may explain the *Chaoborus* length and mass differences observed in my samples during August. Again, larger and heavier larvae were observed in the hypolimnion relative to the epilimnion. This finding is consistent with previous research, which has shown that smaller *Chaoborus*—in particular, 1st and 2nd instars— often reside in the epilimnion because they are less visible than older instars to potential fish predators (Stratton and Kessler 2007).

These observed shifts in *Chaoborus* distribution not only have the potential to affect fish predators, but they also may greatly impact mesozooplankton. Because *Chaoborus* and

mesozooplankton overlapped considerably during August, the opportunity for *Chaoborus* to potentially reduce mesozooplankton was great. Indeed, *Chaoborus* consumption at this time was estimated to range from 53% (when assuming all non-feeding *Chaoborus* at the time of collection never feed at all during the day) to 100% (when assuming all *Chaoborus* feed continuously during the day) of the daily production of mesozooplankton. Further, mean mass-specific crop biomass was higher in August than in either May or November. Given that age-0 planktivorous fish in Hoover Reservoir also rely heavily on mesozooplankton for growth, understanding which assumption (and estimate of consumption) is more realistic is important. My findings are consistent with previous research, as *Chaoborus* are major consumers of mesozooplankton in other reservoirs and natural lakes, demonstrating the ability to severely alter mesozooplankton community composition and distribution (Moore 1994, Stratton and Kessler 2007).

My conclusion that hypoxia is magnifying *Chaoborus'* negative impact on Hoover Reservoir's mesozooplankton community (via increased spatial overlap between predator and prey) is consistent with similar work conducted in other aquatic ecosystems such as Lake Erie (Vanderploeg 2009). Further, Costantini et al. (2008) suggested that increased overlap between predator and prey, owing to loss of prey refuge, could lead to the eventual decline of prey via overconsumption. Thus, a refuge, which mesozooplankton appear to lack during hypoxia, can be critical to mesozooplankton persistence. As mesozooplankton lie near the base of the food web in all aquatic ecosystems, any declines in their availability will influence the entire system, including fish production.

One surprising finding was the estimated impact of *Chaoborus* on mesozooplankton production during normoxic May. At this time, *Chaoborus* density was high (~115

individuals/m^3) and individuals were large (primarily 4^{th} instars). In turn, estimated consumption of the mesozooplankton production was quite high (77%, assuming all larvae with empty stomachs never fed for the entire day, to 148%, assuming all individuals fed continuously during the nighttime). While *Chaoborus* clearly cannot drive mesozooplankton dynamics during the entire year (e.g., in November, its estimated consumption ranged 4-10%, owing to its low density at that time), its potential negative impact on the mesozooplankton community appears high during both spring and summer (and likely early fall, prior to re-mixing of the water column). Given that larvae and juveniles of many ecologically and economically important fishes are abundant in the ecosystem during the time that *Chaoborus* appear to be regulating mesozooplankton, my continued investigation into diet overlap between planktivorous fishes and *Chaoborus* offers potential to help understand *Chaoborus'* potential impact on fish recruitment.

General Conclusions

As shown herein, hypoxia has the ability to cause major changes within reservoir ecosystems, through its influence on species abundance, distribution, and behavior. One of the key species involved in these changes is *Chaoborus*, which, due to its unique tolerance of low DO and its ability to take refuge from fish predators in the hypolimnion, may be as important as a dominant fish such as the gizzard shad in regulating the flow of energy. Importantly, *Chaoborus* appears to have a large impact on the food web during the hypoxic period, which, in eutrophic reservoirs such as Hoover, can last during May through mid-October (Ohio DNR, unpublished data). During this time, hypoxia appears to force overlap in the distribution of *Chaoborus* and mesozooplankton prey, which I estimated could lead to consumption of at least half to all of the mesozooplankton being produced daily. Clearly, such regulation of the zooplankton community would enhance the likelihood for competition for zooplankton prey

resources between *Chaoborus* and planktivorous fish. This negative effect would be expected to be especially great for centrarchid sunfishes such as bluegill, whose larvae 1) are abundant in the system during the period when *Chaoborus* is abundant and hypoxia is rampant and 2) are inferior competitors for zooplankton relative to larval and juvenile gizzard shad (Vanni et al. 2005). While I can only speculate, perhaps both *Chaoborus* and hypoxia are playing a major role in the poor recruitment of bluebill by magnifying the negative impact of gizzard shad on the mesozooplankton community.

Despite evidence in support of my prediction that *Chaoborus* is a driving force in reservoir food webs, other predictions emanating from my hypothesis were not supported. For example, I found no clear evidence that *Chaoborus* act as a net energy sink by transferring available energy from the upper to the lower water column, as larvae did not use the hypoxic hypolimnion as much as expected. In addition, *Chaoborus* consumption of mesozooplankton was estimated to be just as large, if not larger during May, when hypoxia was not present. This finding suggests that it is not simply during hypoxia that *Chaoborus* can have a large impact on the food web.

At this stage, the relative importance of *Chaoborus* versus gizzard shad in regulating the food web in Hoover Reservoir is still somewhat unclear and will require further analysis. To better answer this question, the need exists to quantify mesozooplankton production that is consumed by gizzard shad, as was done with *Chaoborus*, so consumption estimates can be compared between these two important planktivores. Additionally, fish diet analyses will enable me to determine if planktivorous fish are consuming *Chaoborus* during hypoxia, as they overlap in the epilimnion during the day during the hypoxic period. I also recommend tracking the amount of energy secured in the hypolimnion during the summer, as it may be large due to the

larger size of *Chaoborus* individuals at that depth relative to the epilimnion. Despite the need for further investigation, the fact remains that, as expected, gizzard shad are not using the hypoxic layer, while *Chaoborus* are to an extent (which may even be an underestimate as these larvae are known to burrow in sediments; Haney et al. 1990). Quite conceivably then, *Chaoborus* may well be a major driver of energy movement between the bottom and surface layers of the water column.

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TABLES

Table 1. Mean (± 1 standard deviation) temperature, dissolved oxygen concentration (DO), and light levels (photosynthetically active radiation, PAR) for water column layers at two sites in Hoover Reservoir during May, August, and November 2011. Means are averages of results from sites A and B during daylight hours. For May and November, the epilimnion ranges from 0 m to 5 m and the hypolimnion from 5 m to 10 m. In August, the epilimnion ranges from 0 m to 4 m, the hypolimnion from 4 m to 6 m, and the hypolimnion from 6 m to 10 m.

Sampling Month	Water Column Layer	Temperature (°C)	DO (mg/L)	PAR (µmol photons/m^2/s)
May	Epilimnion	14.9 ± 1.3	10.1 ± 1.5	97.8 ± 223
May	Hypolimnion	12.6 ± 0.3	7.3 ± 0.5	0.0019 ± 0.002
August	Epilimnion	29.5 ± 0.7	9.8 ± 3.3	28.40 ± 42.05
August	Metalimnion	27.1 ± 1.3	3.0 ± 1.6	0.22 ± 0.21
August	Hypolimnion	23.2 ± 1.8	1.4 ± 0.2	0.035 ± 0.041
November	Epilimnion	12.4 ± 0.1	5.8 ± 0.2	30.94 ± 50.76
November	Hypolimnion	12.3 ± 0.3	5.7 ± 0.1	0.97 ± 0.12

Table 2. Percent composition of mesozooplankton taxa from all pump samples collected during day and night throughout the water column at sites A and B in Hoover Reservoir in May, August, and November 2011.

Month	% *Daphnia*	% Calanoid	% Cyclopoid	% Rotifer	% Other Cladocerans
May	20.6	34.9	38.7	5.5	0.3
August	7.4	54.6	27.1	10.4	0.4
November	26.8	48.1	17.9	7.2	0.0

FIGURE LEGENDS

Figure 1. Mean temperature (°C), dissolved oxygen concentration (DO; mg/L), and light levels (PAR; µmol photons/m^2/s) for water column layers at two sites in Hoover Reservoir during May (1a), August (1b), and November (1c) 2011. Means are averages of sites A and B during daylight hours.

Figure 2. Total dry biomass (mg/L) of zooplankton important to *Chaoborus* diets during a) May, b) November, and c) August 2011 in Hoover Reservoir, Ohio.

Figure 3. Proportional distribution of *Chaoborus* density (# of individuals/m^3) in the water column in Hoover Reservoir during a) May (day and night averaged), b) November (day and night averaged), c) August (night only), and d) November (day and night averaged) 2011.

Figure 4. Percentage of *Chaoborus* with empty versus non-empty crops in Hoover Reservoir during May, August, and November 2011.

Figure 5. Percent composition of zooplankton dry mass found in the crops of *Chaoborus* collected in Hoover Reservoir during May, August, and November 2011. Also plotted is the percent composition of ambient zooplankton in the water column.

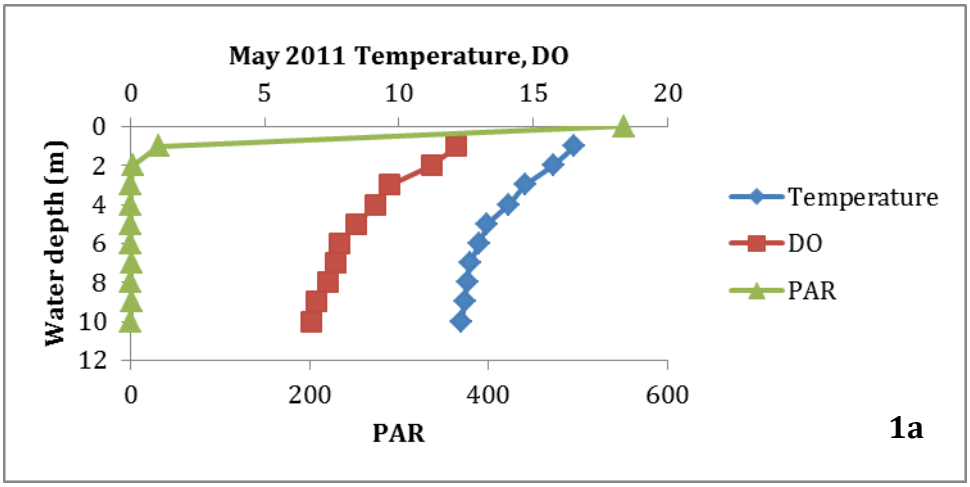
Figure 6. Estimated daily consumption of zooplankton (mg/m^3/d) by *Chaoborus*, both scaled and unscaled, in Hoover Reservoir during May, August, and November 2011. Scaled consumption is calculated from individual consumption multiplied by proportion of non-empty crop and assumes all larvae with empty stomachs never fed for the entire day. Uunscaled consumption is not multiplied by any proportion and assumes all individuals

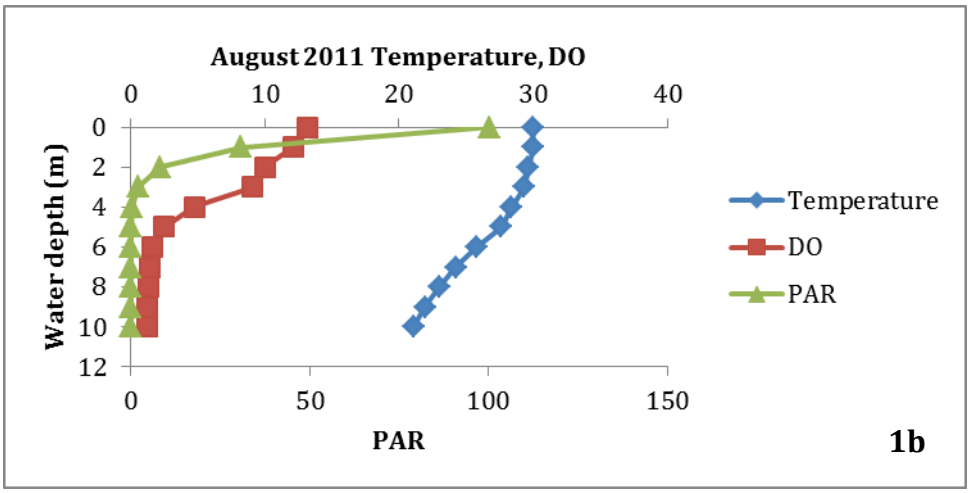
fed continuously during the nighttime. Plotted as well is estimated zooplankton productivity.

Figure 7. Percent composition of planktivorous fish captured via midwater trawling in Hoover Reservoir during May, August, and November 2011.

Figure 8. Percent fish biomass by water-column layer in Hoover Reservoir, Ohio during May, August, and November 2011.

Figure 9. Percent biomass by layer of zooplankton, *Chaoborus*, and fish during both day (left panels) and night (right panels) in Hoover Reservoir, Ohio during May (a,b), August (c,d), and November (e,f) 2011.


May 2011 Temperature, DO
Water depth (m)
PAR
Temperature
DO
PAR
1a


August 2011 Temperature, DO
Water depth (m)
PAR
Temperature
DO
PAR
1b

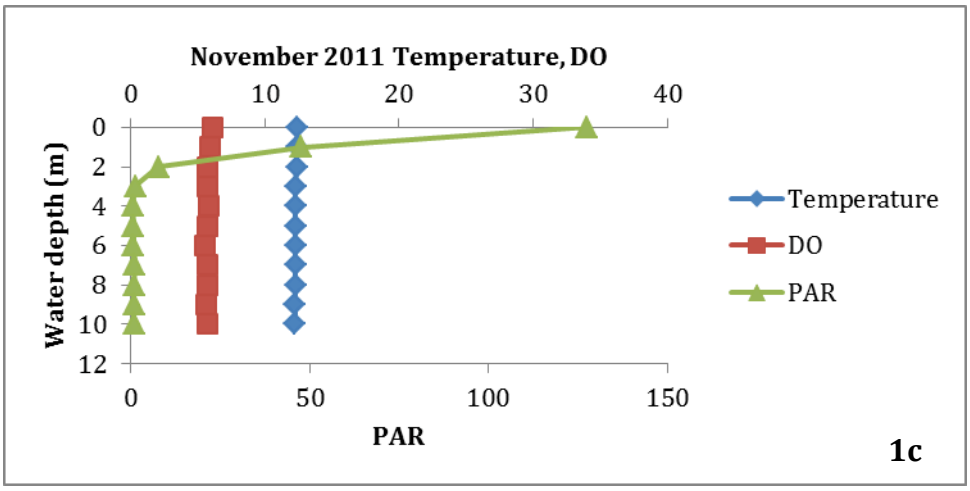
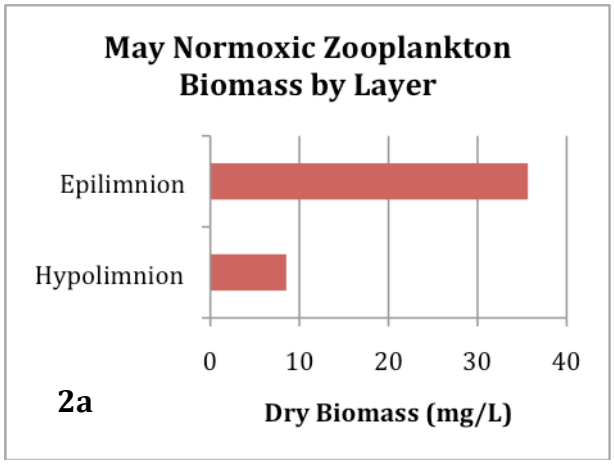
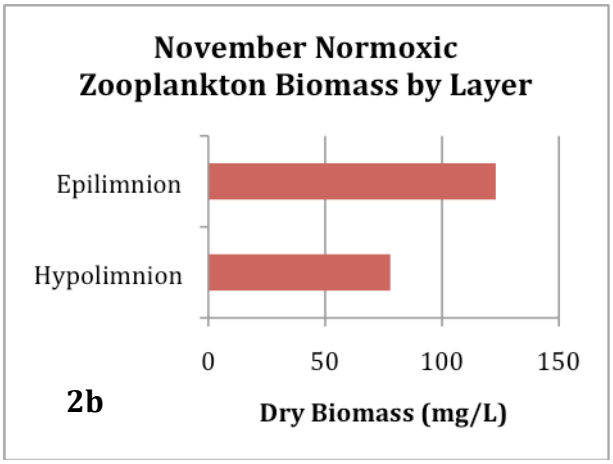

November 2011 Temperature, DO
Water depth (m)
PAR
Temperature
DO
PAR
1c

Figure 1


May Normoxic Zooplankton Biomass by Layer
Epilimnion
Hypolimnion
0
10
20
30
40
Dry Biomass (mg/L)
2a


November Normoxic Zooplankton Biomass by Layer
Epilimnion
Hypolimnion
0
50
100
150
Dry Biomass (mg/L)
2b

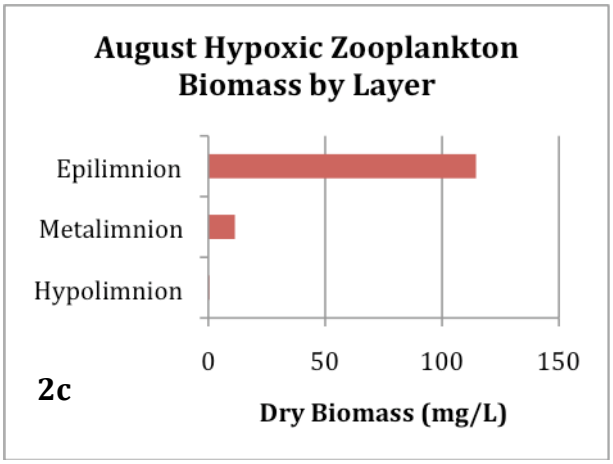
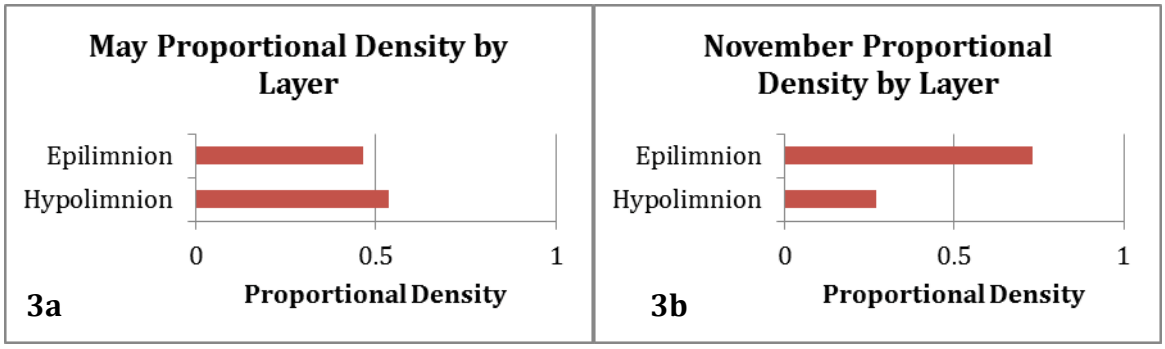

August Hypoxic Zooplankton Biomass by Layer
Epilimnion
Metalimnion
Hypolimnion
0
50
100
150
Dry Biomass (mg/L)
2c

Figure 2


May Proportional Density by Layer
Epilimnion
Hypolimnion
0
0.5
1
Proportional Density
3a
November Proportional Density by Layer
Epilimnion
Hypolimnion
0
0.5
1
Proportional Density
3b

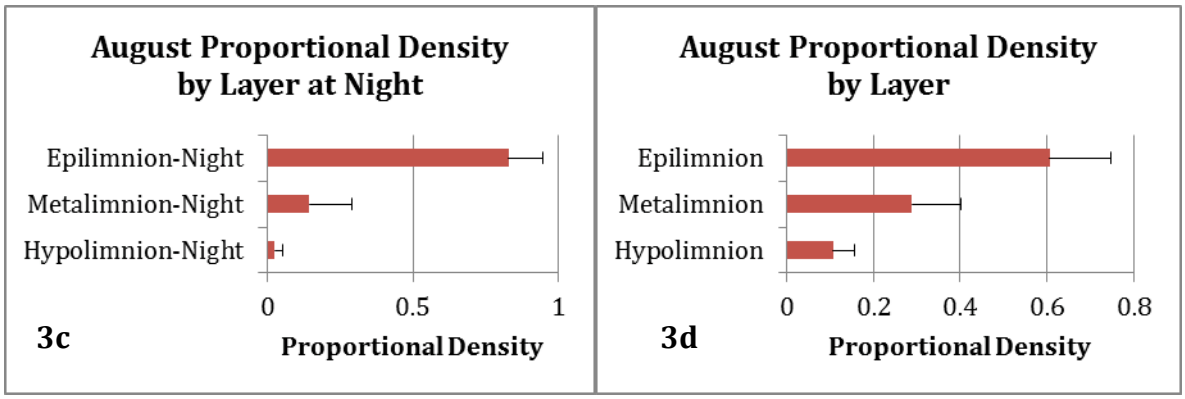

August Proportional Density by Layer at Night
Epilimnion-Night
Metalimnion-Night
Hypolimnion-Night
0
0.5
1
Proportional Density
3c
August Proportional Density by Layer
Epilimnion
Metalimnion
Hypolimnion
0
0.2
0.4
0.6
0.8
Proportional Density
3d

Figure 3

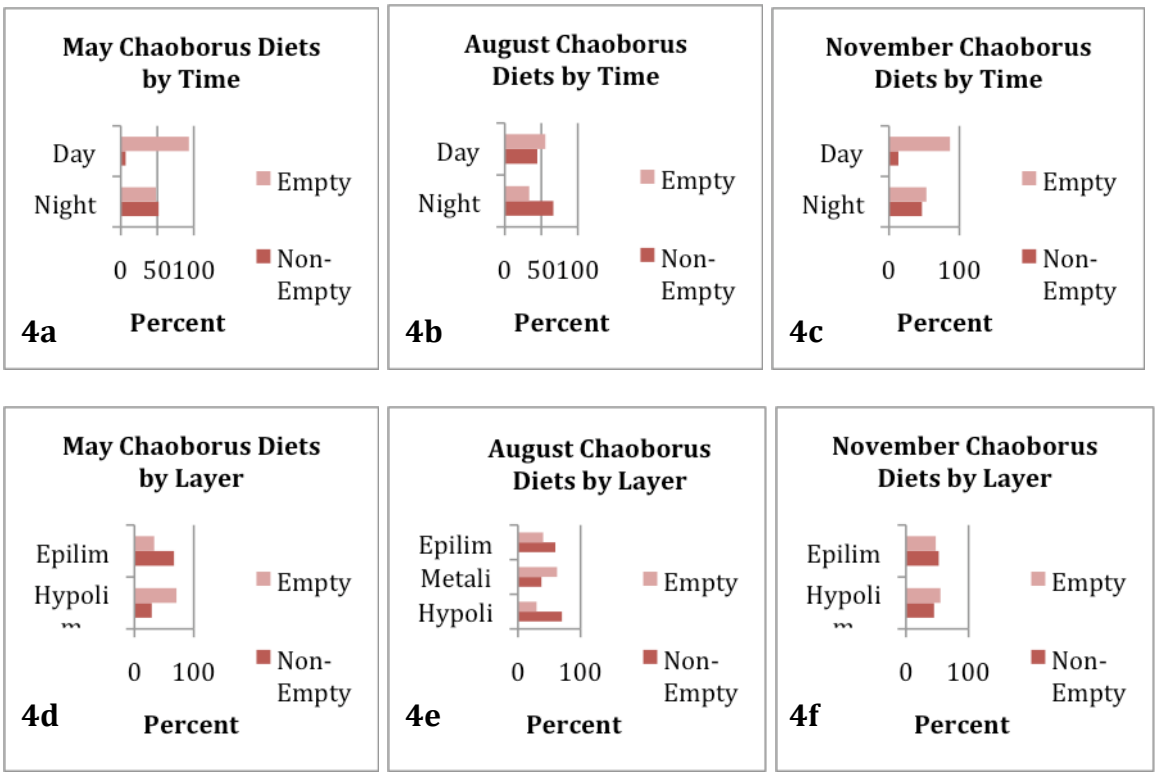
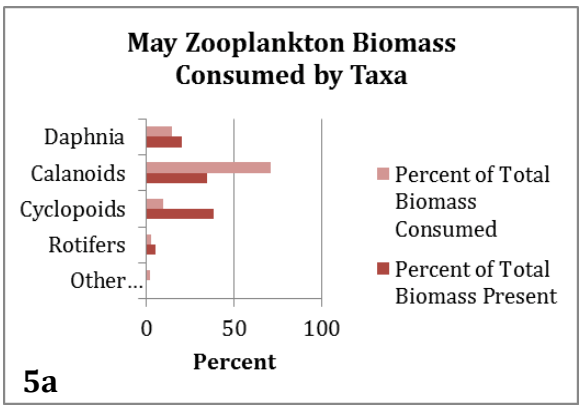
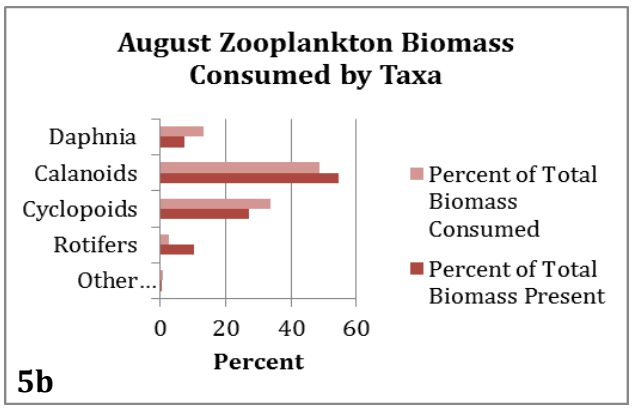

May Chaoborus Diets by Time
Day
Night
0 50100
Percent
Empty
Non-Empty
4a
August Chaoborus Diets by Time
Day
Night
0 50100
Percent
Empty
Non-Empty
4b
November Chaoborus Diets by Time
Day
Night
0 100
Percent
Empty
Non-Empty
4c
May Chaoborus Diets by Layer
Epilim
Hypoli
m
0 100
Percent
Empty
Non-Empty
4d
August Chaoborus Diets by Layer
Epilim
Metali
Hypoli
0 100
Percent
Empty
Non-Empty
4e
November Chaoborus Diets by Layer
Epilim
Hypoli
m
0 100
Percent
Empty
Non-Empty
4f

Figure 4


May Zooplankton Biomass Consumed by Taxa
Daphnia
Calanoids
Cyclopoids
Rotifers
Other…
0
50
100
Percent
Percent of Total Biomass Consumed
Percent of Total Biomass Present
5a


August Zooplankton Biomass Consumed by Taxa
Daphnia
Calanoids
Cyclopoids
Rotifers
Other…
0
20
40
60
Percent
Percent of Total Biomass Consumed
Percent of Total Biomass Present
5b

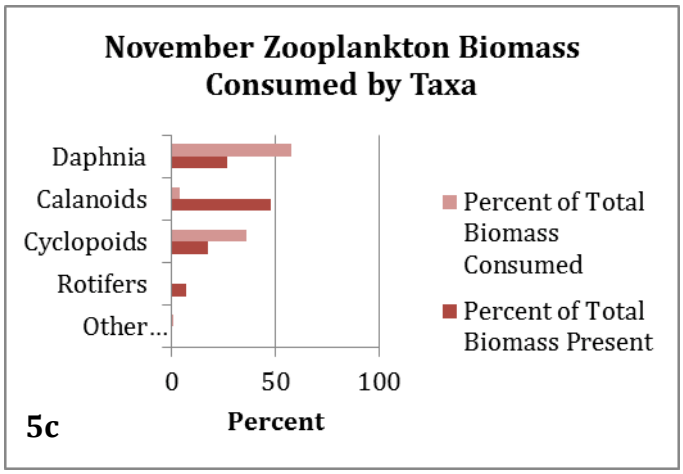

November Zooplankton Biomass Consumed by Taxa
Daphnia
Calanoids
Cyclopoids
Rotifers
Other…
0
50
100
Percent
Percent of Total Biomass Consumed
Percent of Total Biomass Present
5c

Figure 5

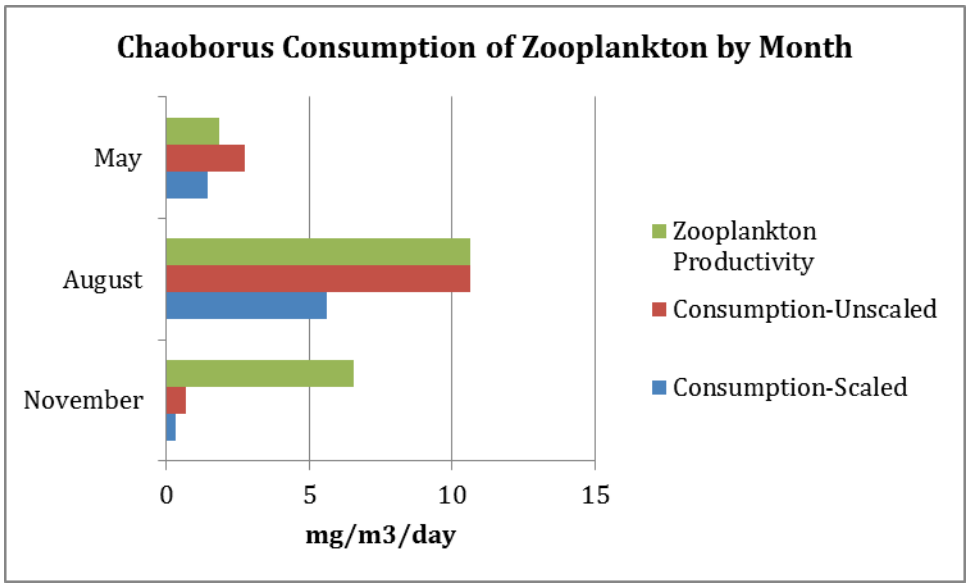

Chaoborus Consumption of Zooplankton by Month
May
August
November
0
5
10
15
mg/m3/day
Zooplankton Productivity
Consumption-Unscaled
Consumption-Scaled

Figure 6

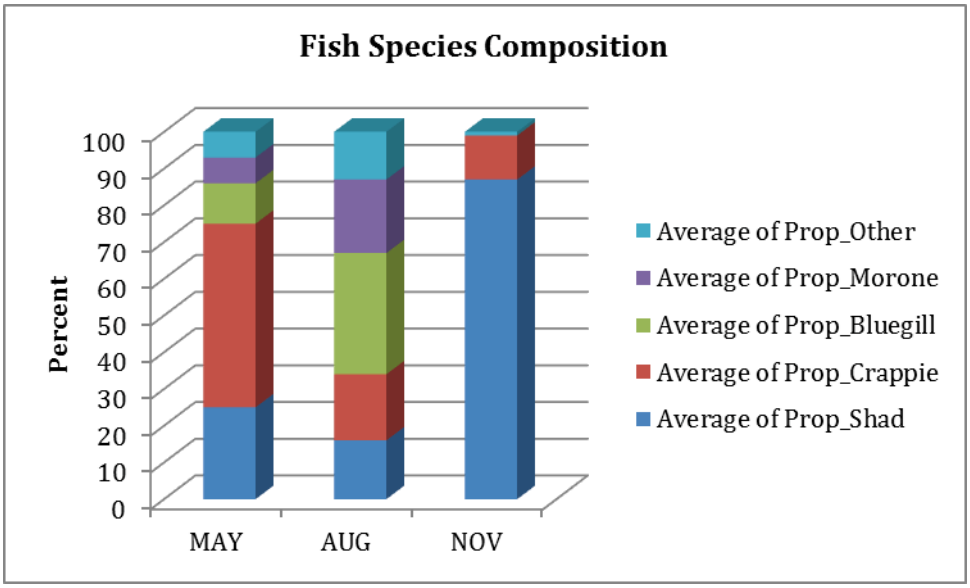

Fish Species Composition
Percent
100
90
80
70
60
50
40
30
20
10
0
MAY
AUG
NOV
Average of Prop_Other
Average of Prop_Morone
Average of Prop_Bluegill
Average of Prop_Crappie
Average of Prop_Shad

Figure 7

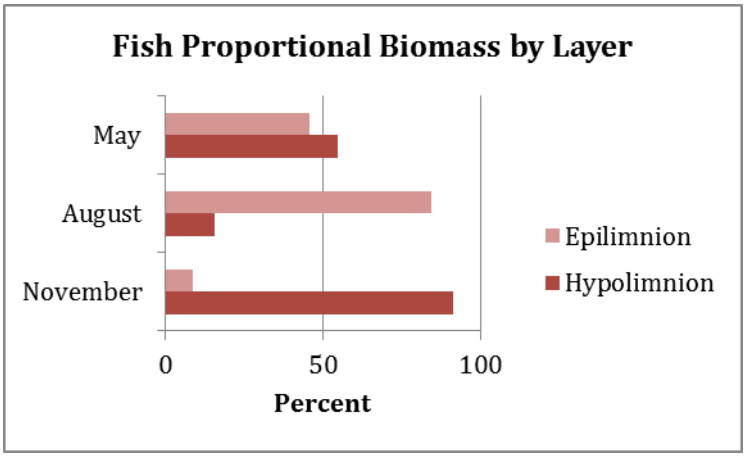

Fish Proportional Biomass by Layer
May
August
November
0
50
100
Percent
Epilimnion
Hypolimnion

Figure 8

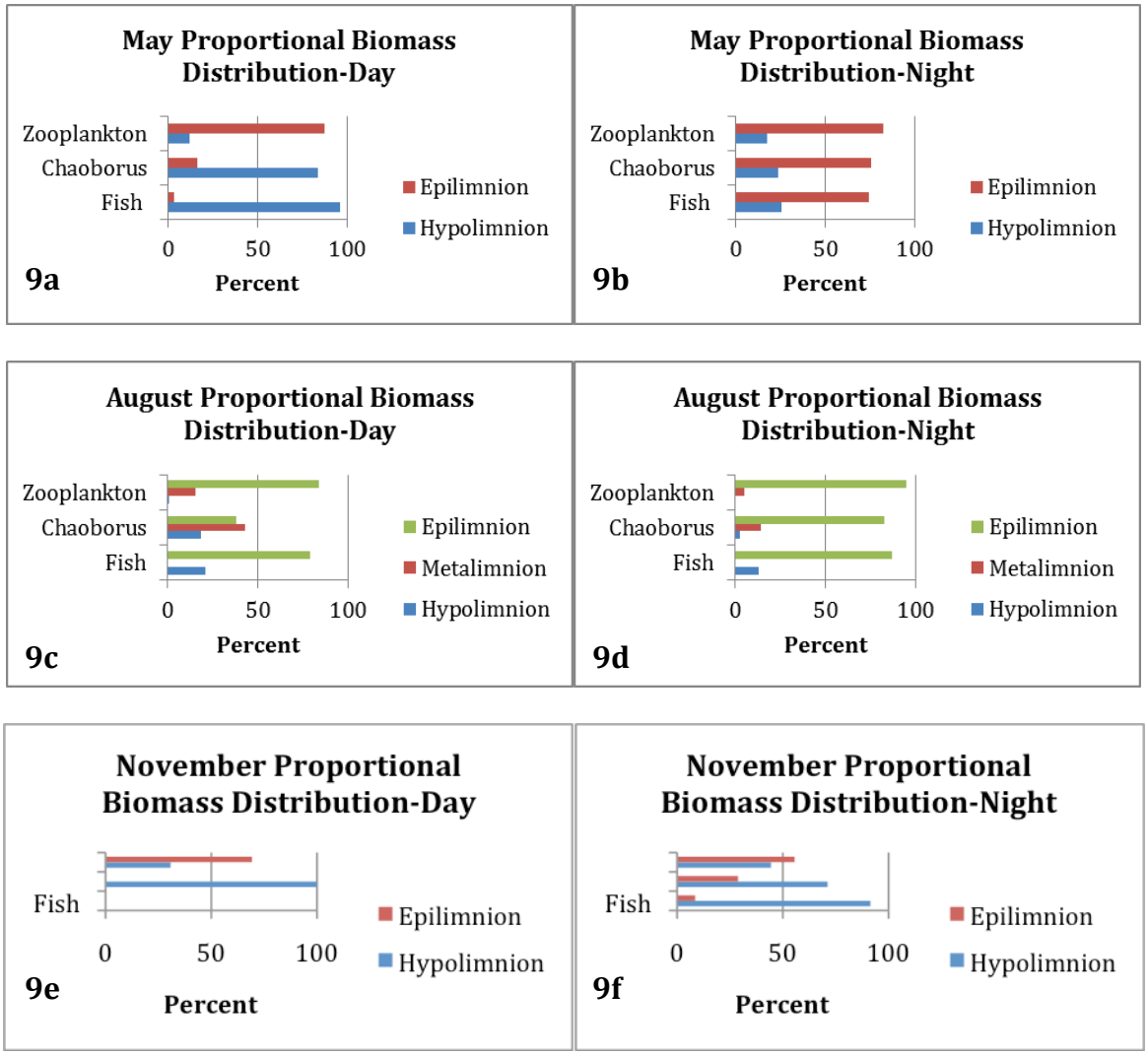

May Proportional Biomass Distribution-Day
Zooplankton
Chaoborus
Fish
0
50
100
Percent
Epilimnion
Hypolimnion
9a
May Proportional Biomass Distribution-Night
Zooplankton
Chaoborus
Fish
0
50
100
Percent
Epilimnion
Hypolimnion
9b
August Proportional Biomass Distribution-Day
Zooplankton
Chaoborus
Fish
0
50
100
Percent
Epilimnion
Metalimnion
Hypolimnion
9c
August Proportional Biomass Distribution-Night
Zooplankton
Chaoborus
Fish
0
50
100
Percent
Epilimnion
Metalimnion
Hypolimnion
9d
November Proportional Biomass Distribution-Day
Fish
0
50
100
Percent
Epilimnion
Hypolimnion
9e
November Proportional Biomass Distribution-Night
Fish
0
50
100
Percent
Epilimnion
Hypolimnion
9f

Figure 9